

SOUND PRODUCTION IN THE SPINY LOBSTER *PANULIRUS* *ARGUS* (LATREILLE)^{1, 2}

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That crustaceans contribute significantly to marine sound is well-known. A list of marine sound producers prepared by the United States National Museum as early as 1942 included members of 17 crustacean families (Fish, 1954). The significance of crustacean sounds to crustacean behavior and to the behavior of other marine animals is, however, largely unknown. There is some evidence that spiny lobsters can detect the vibrations of the sounds they produce (Lindberg, 1955; Dijkgraaf, 1955). Cohen (1955) rejects the statocysts of the lobster, *Homarus americanus*, as auditory organs in the sense of responding to pressure waves in the water, but suggests that statocyst vibration receptors may detect substrate vibrations accompanying sounds.

During June, July and August of 1956, while a guest of the Lerner Marine Laboratory of the American Museum of Natural History, I studied the acoustical behavior of the West Indian spiny lobster, *Panulirus argus*. A study was made of the anatomy of its sound-producing mechanism, and recordings were taken of the sounds produced by this species under various conditions. Through direct observation and motion pictures, data were obtained on the behavior of this spiny lobster in relation to sound production. The study was performed on North Bimini Island, the site of the Lerner Marine Laboratory.

Listening and recording equipment used in the investigation consisted of two Rochelle salt hydrophones, one an AX-58-C, the other undesignated, a Woods Hole Suitcase amplifier or a modified Heathkit amplifier Model A-7C, and an Ekotape tape recorder Model 205. Recordings were made at speeds of $3\frac{3}{4}$ and $7\frac{1}{2}$ in./sec., and were analyzed on a Vibralyzer vibration frequency analyzer at the Woods Hole Oceanographic Institution. Sound-generating equipment employed in the experiments consisted of a Hewlett-Packard audio oscillator Model LAJ or the Ekotape tape recorder, a Craftsman C550 amplifier, and a QBG transducer.

THE MECHANISM OF SOUND PRODUCTION

Stridulation by spiny lobsters (*Palinuridae*) has been described by a number of authors (Möbius, 1867; Kent, 1877; Goode, 1878; Parker, 1878; Heldt, 1929; Parker and Haswell, 1940, p. 455; MacGinitie and MacGinitie, 1949, p. 282; Dijkgraaf, 1955; Lindberg, 1955) and reference to it is found in classical literature (Yonge, 1854, p. 537). The characteristic rasp of palinurids is produced by an

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intricate stridulatory mechanism which has been partially described by Parker (1878) and Dijkgraaf (1955) in a Mediterranean species (*Palinurus vulgaris*). The following description is based on the mechanism as it exists in both males and females of *Panulirus argus*, and adds detail to descriptions previously published of other species.

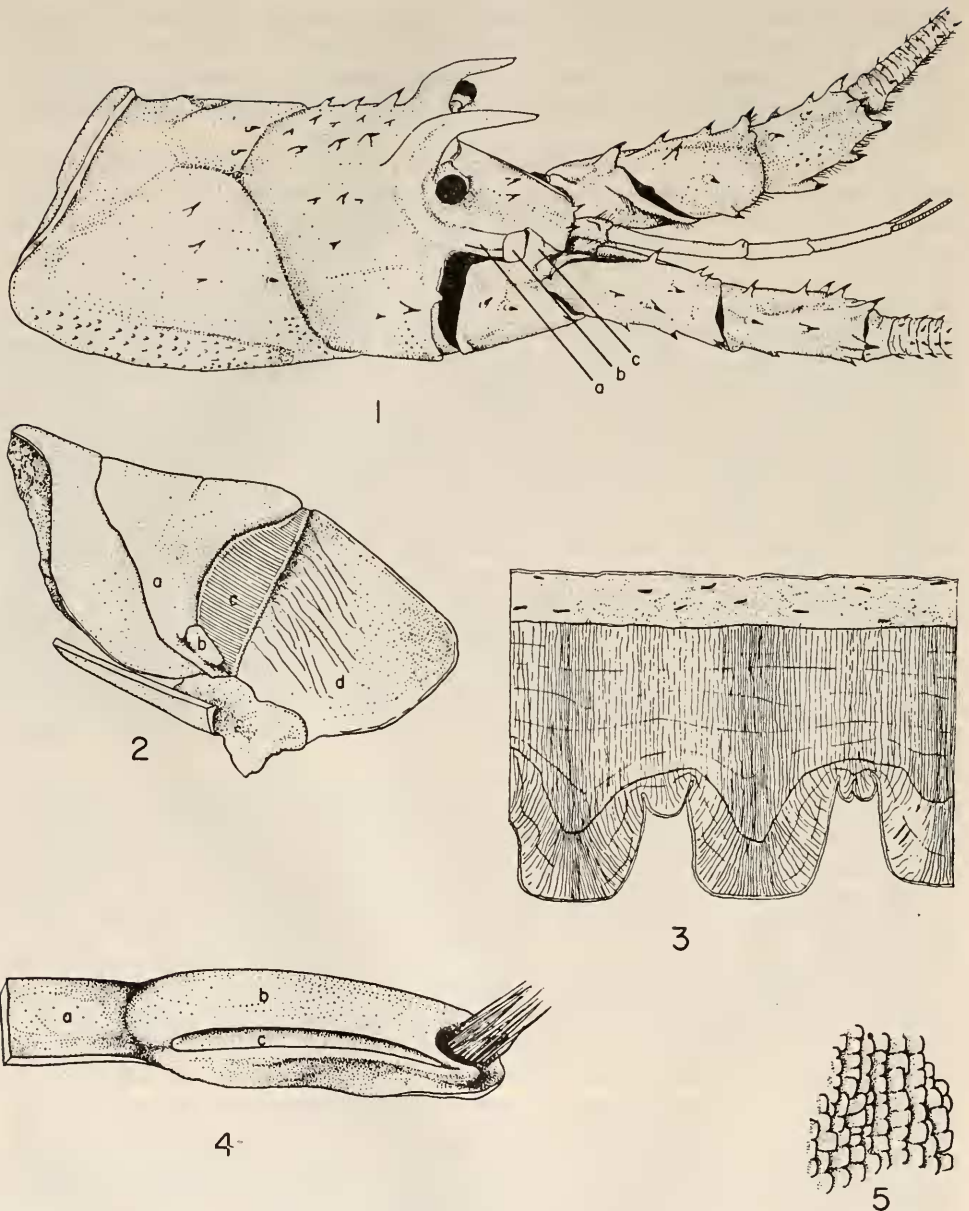
The acoustic mechanism of *P. argus* consists in part of a toothed ridge, orange-colored in life, rising from the surface of the carapace medial to each antennal base and extending anteriorly from beneath each stalked eye (Fig. 1a). A medial process of the basal segment of each antenna fits over the corresponding ridge; as an antenna is raised, a chitinous longitudinally-ridged membrane, the stridulatory membrane (Fig. 2c), forming part of the undersurface of the medial process, moves proximally over the toothed ridge, in the manner described by Dijkgraaf (1955) for *P. vulgaris*, so that a sound may be produced; the sound varies with the rate and force of raising of the antenna.

That a sound is produced only when the stridulatory membrane moves proximally over the toothed ridge—that is, when the antennae are raised—is due to a combination of factors. The medial process of the antenna is itself jointed, the process being divided into a basal flange (Figs. 1c, 2a) firmly united with the basal antennal segment, and a terminal portion (Figs. 1b, 2d) jointed to the posterior edge of the flange. This terminal portion, which Dijkgraaf describes as being a freely-projecting skin-fold in *P. vulgaris*, is covered on its upper surface in *P. argus* with typical exoskeleton. Most of its under surface is formed by a soft chitinous membrane covered with a dense mat of minute setae, the setae becoming sparse along the leading edge of the stridulatory membrane. The under surface of the joint between the basal flange and the terminal portion is the site of the stridulatory membrane.

As a result of the arrangement described, when an antenna is suddenly swept back, the jointed edge of the basal flange bears down on the stridulatory membrane so that the latter is forced to rub proximally over the toothed, orange ridge and a sound is created. Lowering of the antenna relieves pressure on the membrane.

The second factor which determines the effective direction of antennal movement in producing sound is the presence on the portion of the orange ridge over which the stridulatory membrane moves of anteriorly projecting microscopic teeth (Fig. 5) against which the stridulatory membrane is forced when the antennae are swept back. These minute teeth are arranged in shingle-like fashion, teeth of adjacent rows alternating with each other, and the teeth of one row appearing to project from beneath those of the row behind. Anteriorly on the toothed ridge, the leading edges of the teeth form an angle of approximately 60 degrees with the surface of the ridge; in the posterior third of the stridulatory portion of the ridge, the edges are more nearly vertical. Anteriorly the edges of the teeth are slightly serrated; posteriorly they are smooth. In a narrow transition zone (transverse groove between a and b in Fig. 4) between the stridulatory (Fig. 4b) and non-stridulatory (Fig. 4a) parts of the ridge, the teeth give way to blunter microscopic projections, irregularly distributed, which are characteristic of the general carapace.

The presence of the teeth lends to the stridulatory portion of the orange ridge a dull appearance when the ridge is dry; the posterior portion of the ridge, from which the teeth are lacking, possesses a shiny surface when dry. The presence of the teeth can be detected by drawing the tip of the finger posteriorly along the



Stridulatory mechanism of *Panulirus argus*.

FIGURE 1: dorso-lateral view of head region; a) toothed portion of orange ridge, b) terminal portion of medial antennal process, c) basal flange. $\times 1.3$.

FIGURE 2: under surface of medial process of right antenna; a) basal flange, b) guiding knob, c) stridulatory membrane, d) terminal portion. $\times 11$.

FIGURE 3: cross-section of stridulatory membrane. $\times 650$.

FIGURE 4: lateral view of right orange ridge; a) smooth portion, b) toothed portion, c) groove receiving guiding knob. $\times 7$.

FIGURE 5: shingle-like teeth of dorsal surface of right orange ridge (anterior to the right). $\times 500$.

toothed portion of the orange ridge. No difference to the touch between tooth-bearing and toothless portions of the orange ridge can be detected when the finger tip is drawn anteriorly.

The region of transition between the toothed and toothless regions of the ridge is marked by a shallow transverse groove (Fig. 4) which is the posterior limit reached by the stridulatory membrane when an antenna is raised. The action of the stridulatory membrane is guided by the presence of a small knob (Fig. 2b) projecting from the ventrolateral surface of the basal flange adjacent to the lateral end of the stridulatory membrane; the knob during raising and lowering of the antenna runs in a well-defined groove (Fig. 4c) on the lateral surface of the orange ridge. This groove extends as far posteriorly as the transverse groove already described. Behind the transverse groove, the orange ridge gradually flattens to the contour of the general carapace.

That the mat of short setae covering most of the under surface of the terminal portion of the medial antennal process becomes very sparse adjacent to the proximal edge of the stridulatory membrane allows one to observe that the surface from which the setae arise bears a polygonal, usually hexagonal, configuration. In this area individual setae spring from individual polygons; elsewhere, two to several setae arise from each polygon, and the dense mat of setae resulting obscures the underlying membrane.

Parker (1878) has figured a cross-section of the ridges of the stridulatory membrane in *P. vulgaris*. In *P. argus*, this membrane is constructed as follows (Fig. 3): there is a basal stratified layer of squamous epithelial cells. From this layer outward, the membrane is vertically striated to the level of the grooves between ridges, in a pattern which suggests that the major portion of the membrane is comprised of many fused setal processes. The ridges themselves comprise approximately $\frac{2}{5}$ of the thickness of the membrane, and within the ridges, the striations radiate outward to the surface of each ridge. The whole surface of the stridulatory membrane is covered with a thin cuticular layer following the contour of the membrane. In surface view, the ridges are sculptured in a finely polygonal, usually hexagonal, pattern, the size of the polygons decreasing in the direction of the basal flange. Within the grooves between ridges the cuticular border is somewhat folded and the appearance of surface granulation of the ridges is absent. The stridulatory membrane is somewhat flexible, the relatively stiff ridges yielding a rasping sound when the tip of a dissecting needle is drawn across them.

The stridulatory membrane, as seen in cross-section, is also striated horizontally, in a pattern reminiscent of growth lines in skeletal parts of other animals (*e.g.*, tooth enamel, fish scales and otoliths). These horizontal lines continue into the ridges where they are curved in the contour of the ridges.

If the stridulatory membrane and the terminal portion of the medial antennal process are removed, raising of the antenna by hand produces only a slight squeaking sound as the joint edge of the basal flange bears directly on the toothed part of the orange ridge. The spiny lobster itself produces no sound on raising of an antenna so treated, as Parker (1878) also observed.

A specimen of *P. argus* which shed in one of the cement pools of the Lerner Marine Laboratory during the night of August 11-12, 1956, stridulated as usual in the morning, although the general exoskeleton was still soft. No animal from

which the stridulatory mechanism had been removed shed during the summer, so that regeneration of the mechanism cannot be stated as fact.

THE SOUNDS OF *PANULIRUS ARGUS*

The observation of Kent (1877), questioned by Goode (1878), that a shrill squeaking sound is produced by the spiny lobster (*Palinurus quadricornis*) by rubbing together of abdominal segments was probably accurate. During abdominal contractions, after *P. argus* is taken from the water, the abdomen is at times held tightly for a few moments under the cephalothorax, and a rather intense vibration is felt throughout the hand-held animal. At such times a squeaking sound, higher pitched than any antennal noise, may occasionally be heard. The body vibration accompanying this action is similar to that sometimes produced by the lobster, *Homarus americanus*, freshly removed from a trap or tank; while the latter does not produce an audible sound, vibration is at times so intense that an inexperienced person may drop the animal. This matter requires further study.

The antennal sounds of *P. argus* most frequently heard are either a rasp or a slow rattle of longer duration. The slow rattle, recorded during my study only when several animals were confined together in a live car, is seen after vibration analysis to consist of 5 or 6 pulses of sound spanning approximately .5 to 3.3 kc., the rattle lasting about $\frac{1}{4}$ second. The pulses are produced at an average rate of 27/second, varying in several cases from 24 to 31/second. The greatest intensity of each of these pulses lies at approximately .6 kc.

The antennal rasp, which usually accompanies abdominal contractions when a specimen is held in the hand in air or water, is a single burst of sound in which the individual pulses of sound cannot be distinguished. The sound lasts slightly over .1 second, and spans frequencies from below .04 kc. to approximately 9 kc. The zones of greatest intensity lie at .8 kc. and in a rather broad band between approximately 2.5 and 4.7 kc.

As a hand-held animal slows or ceases its abdominal contractions, the antennae may be swept back alternately rather than together. In sounds created by this action, individual pulses can be distinguished on vibration analysis. They are produced at rates varying between 56 and 133/second, with intensity peaks at the levels of the antennal rasp.

The rasp of *P. argus* can be roughly duplicated through moving the antennae upward by hand. The vibration analyses of sounds thus produced are like those of the rasp, except that instead of a single burst of sound there are from four to several bursts at somewhat irregular intervals; the upper peak intensity is more diffuse than in the normally produced rasp, and the lower peak (.8 kc.) of the normally produced sound is lacking. It has not been possible by this method to duplicate the slow rattle recorded from confined animals undisturbed by the observer.

SOUND PRODUCTION AND THE BEHAVIOR OF *PANULIRUS ARGUS*

That the production of sound by the spiny lobster is a response to definite stimuli is indicated by the observations of Lindberg (1955) and Dijkgraaf (1955). The antennae of *P. argus* are frequently moved without the production of sound, even

when the basal segment of the antenna is involved. Aquarium-confined spiny lobsters trained to accept food offered by hand from above during the summer of 1956 characteristically raised themselves on their anterior legs, reaching their antennae up toward the proffered food. At such times, no sound was produced. Similarly, observations on live-car confined animals disclosed no antennal sounds produced during listening by hydrophone at times when the majority of animals were moving their antennae.

Although conditions surrounding production of the slow rattle are obscure, the sound bursts characteristic of the rasp frequently accompany strong, rapid abdominal contractions which are characteristic of the hand-held or net-captured animal. During these contractions, whether the restrained *P. argus* is struggling in the water or in air, the antennae are held back over the body and each forward thrust of the rapidly and forcefully contracting abdomen is accompanied by a brief rasp as the stridulatory membrane rubs over the orange ridge. Sounds intermediate between the slow rattle and the rasp are produced by antennal movements in the absence of abdominal contractions; although these intermediate sounds are difficult to distinguish by ear from the rasp, vibration analysis distinguishes them.

It is evident that the sounds produced by *P. argus* and the behavior which they accompany differ with circumstances. Dijkgraaf describes production of the rasp during struggling between two individuals of *P. vulgaris*. Circumstances under which the rasp is produced in *P. argus* (grasping in the hand, capturing in a net, injury) suggest that this sound is related to defensive behavior. This relationship is further emphasized by the fact that during production of the rasp, the spiny antennae are held over the back, tightly depressed against the carapace or against the grasping hand. During abdominal contractions, the forward-directed spines of the carapace are driven against the hand, and the hand is driven against the backward-directed spines of the antennae; blood is frequently drawn. At the same time, the abdominal contractions provide an efficient scissor-like action through the sharp edges of the abdominal exoskeleton, and the fingers caught within the scissors may be cut. Presumably the action described would also be performed against natural captors in the sea.

Gradual subsidence of abdominal contractions and of antennal sound by the hand-held animal will take place. A sudden movement of the hand will, however, re-initiate the whole process, and again a gradual subsidence, usually through a period of alternate antennal stridulations, will occur. The response gradually diminishes.

At the Lerner Marine Laboratory, up to several dozen spiny lobsters are confined at a time in a live car of screen and boards adjacent to the Laboratory dock in Bimini Harbor. When a hydrophone was lowered into this live car and left hanging in it during the daytime, the slow rattle already described was frequently heard. The individual pulses of the slow rattle, probably produced as the stridulatory membrane skips along the orange ridge, can be detected. The sound does not necessarily accompany marked activity of the animals to judge from visual observations, and is not recorded from a highly active animal. This slow rattle seems to be more in the nature of a conversational sound, as compared with implications of argument suggested by circumstances under which the rasp is produced.

The slow rattle could not be heard with the equipment employed 30 feet from the live car, although the rasp was clear over this distance underwater.

That the slow rattle is not produced by accidental movements of the antennae is suggested by the following observations: if the spiny lobsters in the live car were stirred up with an oar neither the slow rattle nor the rasp was heard, and after this procedure it was some time before the slow rattle was heard again; nearly constant antennal movements by isolated animals moving about in glass aquaria did not result in production of any sound, nor was the slow rattle recorded from any isolated animal; the slow rattle was recorded only during daylight, not at night when the spiny lobsters were moving about the live car; if an animal were suddenly clamped to the bottom with the edge of a dip net, only the rasp was heard to accompany the animal's activity, never the slow rattle which might have been anticipated if it were an accidental sound.

During the daytime, undisturbed *P. argus* tended to remain heaped in the corners of the live car; at night the animals were more obviously active, moving about the screen forming the sides of the car. Yet the slow rattle was heard only during the daytime. Thus, during 1½ hours of listening between 0900 and 1100 the morning of 21 June, the slow rattle was heard 76 times, whereas it was not heard at all during comparable time between 1950 and 2130 the evening of 20 June under an approximately ⅝ full moon. These observations were made when the live car contained between two and three dozen animals.

The stridulatory mechanism is best rendered inoperative by bilateral removal of the medial process of the antenna, at the junction of the basal flange and basal segment of the antenna. It is difficult effectively to remove the stridulatory membrane without removing the whole medial process, since even a remnant of the ridges will produce considerable sound.

A male spiny lobster with the stridulatory mechanism bilaterally removed was confined in an aquarium with a normal male of similar size during July of 1956. The normal animal was the dominant individual, frequently approaching the operated animal head-on with extended anterior walking legs and slightly raised antennae, walking forward as the operated animal retreated to a corner. At such times, no sounds were heard.

Numerous attempts to influence the behavior of spiny lobsters by playing recordings of the rasp and of the slow rattle into the live car and into aquaria containing individual specimens were unsuccessful, nor did recorded sounds of spiny lobsters played underwater noticeably alter the distribution of various fishes confined with them. The same was true if pulsating signals generated with the audio oscillator set at 17 to 40 cps. (Moulton, 1956) were played into the water.

DISCUSSION

The production of two characteristic sounds by *Panulirus argus* and the behavior which the sounds accompany, parallel a situation occurring among fishes in sea robins (*Prionotus* spp.) which when free during the breeding season produce a staccato call, but which when disturbed in various ways produce a vibrant grunt of other frequency characteristics (Moulton, 1956). Like the staccato call of the sea robins, the slow rattle of the crayfish has not been recorded from hand-held or otherwise disturbed specimens. As the grunt and the staccato call of the sea

robins relate to two different patterns of behavior, thus the rasp and the slow rattle of the spiny lobster, *P. argus*, do also.

The significance of their sound production to the survival of spiny lobsters is unknown. Lindberg (1955, pp. 178-179) observed that *P. interruptus* did not stridulate unless it and an attacking fish touched each other. Since the sounds produced by *P. argus* span the frequency sensitivity of various fishes which have been tested (Kleerekoper and Chagnon, 1954), it is not impossible that a combination of sound production and injurious strokes of the abdomen may combine as a deterrent to predators. Unfortunately, information is lacking on this point. My own observations concur with those of Lindberg in denying an obvious effect of the rasp on fish behavior. A mutilated specimen of *P. argus* passing, while vigorously rasping, through approximately 25 feet of clear water at Bimini on the west side of Turtle Rocks, did not immediately nor during several minutes of observation through glass panels at the surface attract any of the numerous reef fishes feeding within the zone of observation, nor did visible fishes which might be anticipated to feed on injured spiny lobster noticeably alter their behavior.

Dijkgraaf's (1955) observation that stridulation could be induced in a highly excited *P. vulgaris* by imitating the rasp adjacent to the aquarium is compatible with Lindberg's observation that *P. interruptus* moved away from other animals forced to stridulate nearby but out of sight. Lindberg observed that stridulation occurred only upon impending conflict and thus considers the sound "a threat rather than an alarm." Several *P. argus* contained in aquaria at Bimini moved rapidly away from a net or grasping hand, but did not stridulate until grasped or captured in the net—that is, the rasp was not necessarily produced during rather violent escape maneuvers.

The failure of fishes to respond to the sounds of *P. argus* is consistent with previous observations on the responses of free fishes to sound generally (Moulton and Backus, 1955; Moore and Newman, 1956). Since, however, several kinds of fishes will respond initially by quickened swimming movements—startle reactions—to sounds which later will fail to affect their behavior, it is possible that a sudden rasp by a mouth-held palinurid might cause a preying fish to release its hold and thus its prey, particularly if the sound were accompanied by strong abdominal contractions. This is to suggest that the rasp may act as a double assurance mechanism.

Vibration analyses of various fish sounds recorded from identified species at Woods Hole and Bimini indicate that sounds produced by several kinds of fishes under duress of various types are more like the rasp of the spiny lobster than like the slow rattle of undisturbed *P. argus* or than like the staccato call of free sea robins during the breeding season. The burst of sound characterizing the spiny lobster rasp also characterizes the sounds produced, during handling, by sea robins (*Prionotus* spp.), grouper and hind (*Epinephalus* spp.), angelfish (*Pomacanthus* spp. and *Angelichthyes ciliaris*), squirrelfish (*Holocentrus ascensionis*), triggerfish (*Balistes vetula* and *Melichthyes piceus*), swellfish (*Spheroides* spp.), porcupinefish (*Diodon hystrix*), a jack (*Caranx hippos*), and grunts (*Haemulon* spp.)—defensive behavior of all of these includes production of sounds lacking sharply defined individual pulses within the limits of the analyses. Thus sounds produced in a variety of ways—by stridulation of skeletal parts, by muscle contraction against an air bladder or adjacent tissue, by pounding of pectoral fins against the body—

but under similar circumstances, present similar, although not identical, vibration analyses. These observations, combined with observations on the slow rattle of *P. argus* and the staccato call of sea robins, suggest that while sounds produced by undisturbed marine fishes and crustaceans are likely to be sounds comprised of individual pulses of brief duration, sounds of marine fishes and crustaceans under duress are more likely to be bursts of sound of longer duration in which individual pulses are obscured or absent.

Another category of marine sound, comparable in its vibration analyses to sounds produced under duress by fishes and to the rasp of the spiny lobster, is the feeding noise of such fishes as wrasses (*Labridae*), porcupinefish, swellfish, triggerfish, and angelfish. If sound bursts comprise threats or alarms, as conditions of their production would suggest, noisy eating by these organisms may serve to repel rather than to attract predators.

Exceptional in producing sounds of sharp individual pulses during defensive behavior are representatives of two crustacean groups in the Bimini area, the stomatopod (*Gonodactylus oerstedii*) and several kinds of snapping shrimp (*Alpheidae*), especially *Alpheus armatus* and *Synalpheus* spp. (Pearse, 1950). Although produced in a different way, the sound of the mantis shrimp is like that of the snapping shrimp (Goode, 1878; Johnson, Everest and Young, 1947; Fish, 1954), and their vibration analyses are indistinguishable. Both are either burrowers or symbionts of organisms providing highly protected situations (Pearse, 1950; Townsley, 1953; Banner, 1953; Clarke, 1955). Further, the sounds produced are the by-products of accompanying movements which have a distinctly protective value—the decisive closure of the snapping shrimp large chela with its accompanying squirt of water (Schmitt, 1931, p. 192; Johnson *et al.*, 1947) and the stinging extension of the raptorial appendage of the mantis shrimp.

That some sounds of marine arthropods are other than accidental is, however, clearly indicated by the intricate stridulatory mechanism found among the spiny lobsters (*Palinuridae*). The usefulness of the sounds produced, as of the sounds produced by many kinds of fishes, is yet to be determined.

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SUMMARY

1. The intricate stridulatory mechanism of the West Indian spiny lobster, *Panulirus argus*, and the sounds it produces are described. The sounds are related to various patterns of behavior.

2. On the basis of behavioral evidence it is suggested that a slow rattle is characteristic of spiny lobsters when contained in groups, and that a rasp is a usual component of defensive behavior.

3. The characteristics of the sounds of *P. argus* are compared to those of other marine sounds of biological origin. On the basis of this comparison, an attempt is made to generalize (a) the type of sound which accompanies defensive behavior of marine fishes and crustaceans, and (b) the type of sound stemming from marine fishes and crustaceans when undisturbed.

4. It is concluded that the intricacy of the sound-producing mechanism of *P. argus*, and of other palinurids, justifies a conclusion of a significance of sound to the biology of spiny lobsters. While certain suggestions of a possible value of the rasp to survival of spiny lobsters are presented, a consistent effect of the rasp on the behavior of other spiny lobsters and on predator organisms has yet to be demonstrated.

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